

IN DEFENSE OF THE CONCEPTS OF MAJOR AND MINOR HABITATS IN APPROACHING BIOLOGICAL PROBLEMS ¹

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One of J. Speed Rogers' principal concerns in his studies of the craneflies was the correlation of the distribution and abundance of the adults and larvae of the species with various natural situations. I, among others, began my investigations of aquatic insects along these same lines; and the concepts of major and minor habitats, as developed by Rogers (1933, 1942, and elsewhere) have continued to prove helpful and productive. I do not, of course, presume to claim priority for Rogers in regard to these terms, but certainly he gave them a peculiarly Rogersian turn; and the farther I have progressed in my own investigations, the more central some of Rogers' ideas have become in my thinking concerning the biology of insects. Since some ecologists have criticized the habitat-approach or labelled it unproductive while others have developed similar or quite unrelated concepts in connection with their studies, the appearance of a Rogers' memorial volume seems an appropriate place to reconsider the ideas of major and minor habitat.

The concepts of major and minor habitats are, in my thinking, focal points for organizing data. Before turning to more theoretical considerations, I want to outline briefly some of the facts and certain logical deductions from them concerning the relationship of distribution and abundance in a specific insect in order to give the reader some idea of the type of data on which I plan to base further discussion. For this purpose I have selected *Tropisternus mexicanus*, a medium-sized hydrophilid water beetle, which is currently the subject of intensive investigation.

The problems concerning the distribution of *T. mexicanus* are both taxonomic-genetic and ecological, but the two approaches cannot be clearly separated. For example, the range of the species as a whole extends from Central America to Cuba, north to Indiana and New York. Within this area, however, five distinct subspecies are recognizable on the basis of color pattern each associated with a distinct set of climatic conditions, soils, and vegetation. There

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is evidence from experiments, however, that the differences in color pattern are genetically controlled and not simply due to environmental influences.

In a general way, the coloration conforms to the Allen-Gloger rule. That is, dark forms are associated with humid climates while light forms are found in arid-hot regions. Other elements of the pattern, and other characters do not conform so that a simple ecological correlation seems to be excluded. Ecological factors, however, seem to influence gene flow from one population to another, and conversely the genetic composition of the populations in different parts of the range undoubtedly influences physiological tolerances.

In the United States three subspecies of *mexicanus* have been recognized: (1) Typical *mexicanus* ranges in the United States from the Mexican boundary to Missouri in a narrow strip west of the Mississippi River. In Oklahoma, Kansas, and Missouri the typical form intergrades (on the basis of color pattern) with (2) *striolatus*, which ranges over the states east of the Mississippi south to southern Georgia and western Florida. In the latter area *striolatus* intergrades with (3) *viridis* which is confined to Florida and extreme southeastern Georgia.

This is admittedly an oversimplified model of the population structure within the U. S. segment of the species. The distribution in the areas outlined is obviously not continuous, and there are indications in places of local populations isolated from the main areas of occupation. But nowhere is the distribution random; both frequency of occurrence and abundance center around certain types of aquatic environments. It is only during flights of the adults under relatively windless conditions that we might imagine a random distribution with the numbers of individuals decreasing logarithmically from the larval breeding places.

In defining the types of situations in which the forms of *T. mexicanus* occurs it is necessary to keep in mind several important facts about the biology of the species. The larvae are aquatic predators and scavengers feeding on mosquito larvae and other aquatic insects either alive or dead. The adults, however, are algophages and scavengers which only rarely take live food.

Further, the dispersal of the species is accomplished by flights of the adults which are apparently conditioned by temperature and humidity, but seem also to be influenced to some extent by the

drying up of the situation in which they find themselves. The western limit in the U. S. may be fixed by the degree of humidity needed to induce the adults to disperse, and this same effect may account for the failure of the species to follow up the permanent streams into drier regions. The inward curve of *mexicanus* in Missouri may reflect the interaction of humidity and lower temperatures, while the greater extent of habitat occupancy in Florida may represent the other extreme.

Therefore, the habitat selection by the beetles or the beetle selection by the habitat is primarily conditioned by such variables as the presence of suitable larval food, suitable adult food, and suitable recurrent atmospheric conditions to allow the dispersal of the adults. Many other conditions also affect the organisms, of course, such as the presence of predators in relation to shelter, suitability of the surrounding soil for pupation, vegetation for attachment by the larvae and depositing of eggs in relation to currents, temperature extremes, and so on. The conditions of the soil during pupation may be the critical factor in regard to final pigmentation of the adults.

The distribution of the subspecies can be further correlated to some extent with other differences in habitat. The typical form is found most frequently and abundantly along the margins of streams, in backwaters, in pools, in drying stream beds, and in small pools or ponds near streams. The subspecies *striolatus* occupies very similar situations within its range, but is found most frequently in the backwaters of large streams and less frequently in temporary pools. In Florida and southeastern Georgia, as one might expect, *viridis* occurs much more frequently in permanent lenitic situations. It has not, however, forsaken the stream environment as completely as I once thought, and the frequency of the form if not its abundance seems to be greatest where the water is gently flowing.

I believe that the correlation of observations on habitats is beginning to produce concepts which are important in considering not only the ecology but the taxonomic-genetic relationships in this species. The model of the population structure of *T. mexicanus* must take into account the nature and distribution of habitats as well as the more general environmental influences. I think it can best be visualized now in terms of many small breeding areas in which local conditions are influenced by the broad environmental

aspects. The connections between these situations are in time not space.

There are still many things to investigate in regard to this problem, but it looks as if we can now begin intensive investigations of the individual factors in the laboratory. How did we reach this point? Certainly not by sitting down and considering the individual factors abstractly, nor even by examining them experimentally in the laboratory. There are too many variables to allow anyone to select the critical points *a priori*. The day may come when biologists using suitable calculating machines and punch cards can attack any problem at random, but that day seems farther and farther off the more we learn of the intricacies of life. What we need today are techniques for digging out worthwhile problems, without depending entirely upon intuition.

The basic data on which I have based deductions about *T. mexicanus* come from the correlation of notes in my field catalogs supplemented by examination of specimens and some experimentation in the laboratory. In accumulating the mass of field notes I have, following a precept of Rogers, asked myself every question I could think of about every situation in which I have collected. The answers to these questions *are* my field notes. The questions concentrate on two concepts: (1) Can I detect anything I can equate with *major habitat*? (2) Are there local details which indicate more specific relationships of the organism with this environment? Or in other words, what are the *minor habitats* or subdivisions of this situation?

Much of the information acquired in this way is probably utterly worthless. Some is too subjective to quantify; some seems to have no bearing on any problem in which I am interested. As far as I can find, however, no one has found a better way to start digging into a complex problem involving a single species, an association, or a region.

I hope that I have been able to point out in the preceding discussion some of the kinds of problems to which the habitat-approach may contribute. The fact that neither the approach nor the problems are currently in style in ecology seems to me wholly immaterial.

We can, of course, approach biological problems from other directions and on other levels. We can completely generalize the concept of habitat by defining it as a portion of the biosphere in

which the physical and biotic factors are such that the organism or organisms with which we are concerned can establish, maintain, and reproduce a population. We ought to realize, however, that this is a generalized inductive abstraction which was derived from a mass of data accumulated on an entirely different level. The question is not whether the definition is sound, but whether it can be used as a basis for further investigation.

In contrast, the concept of major habitat is an abstraction at quite a different level. Our primitive ancestors must have clearly perceived the correlation between the occurrence of certain animals and various types of terrain and vegetation, because such perception was vital both from the point of view of food getting and survival. Many living men develop a remarkable ability to recognize the probable habitats of certain animals in which they are interested, and although this "art of the hunter" is difficult to explain the investigations of modern psychology indicate that it is essentially a learning process involving inductive-deductive reasoning.

Unfortunately, the process by which such discriminations are made are usually not recognized by the subject. The result is that there is little possibility of standardization in any scientific way until we know considerably more about the learning process involved. Nevertheless, the breaking up of a complex area into subdivisions for the purpose of preliminary investigations of the fauna and flora is invaluable as a starting point, and a highly subjective "feeling" for "habitat" has been the classical approach to descriptive ecology.

In order to subdivide the environment with some greater degree of objectivity, however, we need to recognize some general criteria for the recognition of subdivisions. It seems obvious that a general definition of habitat is on too high a level—a level on which we simply cannot work in our present state of ignorance about physiological tolerances and biotic interrelationships. We need a tool which does not rely initially upon detailed information, unless we are content to await the accumulation of the necessary facts.

The concept of major habitat has served for many years as such a tool for the study of both individual species and communities. In a restricted sense we may define it as *a typical, more or less frequent, feature or complex of topography, drainage, soil, and vegetation* (Rogers, 1933). I would qualify this only by adding that the unit should be refined as far as available data permit. We must

keep in mind in using such a unit concept, however, that we have abstracted a portion of the total environment and induced an apparent stability in a dynamic process; and we should be ready to abandon our brainchildren when a better way of dealing with the facts is found.

Furthermore, we should realize that our concepts of major habitats must be derived for a particular area and for a specific purpose. The unreality of specific examples becomes apparent when we try to transfer them from one region to another. The discovery that the major habitats of water beetles as I conceive them in Florida is only vaguely applicable to conditions in Michigan and Indiana does not bother me, because I realize that in the first place I was seeking a means of simplifying a complex of factors the permutations and combinations of which must be almost infinite. They do give me basis for comparison. It is too much to expect that any two natural situations even within a small area are exactly alike in all respects because the ecological relationships of organisms have time as well as space depth. We can only hope to catch certain situations in a state which may be partially repeated in time under the general conditions of the region.

The test of a tool, however, is not whether it can do everything, but whether or not it can produce the end results for which it was intended. In this respect the concept of major habitat needs further testing, but it has already made valuable contributions in the organization of great numbers of facts. Much of the material in the *Naturalist's Guide to the Americas* (1926), for example, is organized around major habitats or natural regions. The value of such a work cannot be denied, even if we question its philosophical basis. It is only unfortunate that there are not more such outlines to help the field ecologist to select the problems worth attacking.

The major habitat concept is most valuable in dealing with large animals and with vegetation. With smaller animals we need a more refined tool. This is particularly true if we are concerned with the distribution and abundance of species. The *specific habitat* (Rogers, 1933) and the *characteristic minor habitat* seem to be useable concepts in regard to specific organisms. When conditions are such that minor habitats are regularly telescoped upon one another or are bound together in some way, the *micro-habitat* of Shelford is applicable.

In regard to species or closely related groups the minor habitat concept involves the assumption that *every organism has some particular set of environmental conditions under which it best establishes, maintains, and reproduces a population*. The further assumption that minor habitats like major habitats can be recognized by indicator conditions is inherent in the idea and distinguishes it from the *niche* of Elton. In a sense, the major habitat serves as a matrix in which minor habitats are enclosed. The occurrence of a major habitat, however, does not assure the occurrence of a particular minor habitat, nor can the reverse be proven.

The assumption on which the minor habitat concept is based can be tested to some degree by making logical deductions about the consequences and checking them against observed conditions. For example, we generally make the observation that when mosquitoes are abundant in a situation, some suitable breeding place (minor habitat) is close by. This assumption of a specific minor habitat for each species has been widely used in malaria control with great success. In many other cases both frequency and abundance of organisms can be directly correlated with the occurrence of specific habitats. The reverse of this process is, of course, the inductive basis of the concept.

It is repeatedly observed with water beetles that certain types of situations are regularly correlated with the occurrence of certain species or groups of species. For example, in Michigan *Agabetes acuductus* occurs frequently and abundantly in seasonal woodland pools where decaying deciduous leaves are abundant. It also occurs frequently but less abundantly in the shaded margins of swamps, bogs, and larger bodies of water where small local areas present conditions of leaf-fall and shading similar to those in the woods ponds. In western Florida, over a thousand miles to the south, *Agabetes acuductus* occurs in very similar woods pond situations in association with a number of other typical woods pond species also found in Michigan, (Young, 1955).

The repeated observation of correlations such as those cited above leads to the assumption that similar minor habitats may occur even in places where they are not recognizable by indicators. They may be interrelated as zones, patches, or mosaics in complex major habitats, and in aquatic beetles this may be the explanation of the occurrence in close spatial proximity of species which seem to occupy identical ecological niches.

J. R. Zimmerman (unpublished ms.) has recently been able to show that beetles of the genus *Laccophilus* show distinct "habitat preferences" even when several species occur in the same small pond. That is, the distribution is not random even within a very small aquatic situation, but can be correlated with depth of water, type of bottom, and other recognizable features even though the "ultimate" causes of the restrictions are not yet apparent.

In most natural situations ecological relationships are so complex that any attack which offers the possibility of simplification for initial analysis seems worth trying. Elton (1927) and others have pointed out that the inter-relationships of many organisms are most profitably studied on small islands, in the arctic, or under other extremes of environmental conditions. The minor habitat often presents extreme conditions, and it is perhaps for this reason that the study of certain extreme situations such as those of bogs, brackish water, and cold and hot springs has proven profitable in understanding the distribution of certain species.

Paulian (1948) has arrived at a very similar conclusion in regard to the usefulness of the minor habitat concept. Unfortunately, he uses terms which make a confusion with the *ecological niche* of Elton inevitable, and although it seems niche and minor habitat overlap I do not think that the two should be equated at present. Minor habitat might be thought of as a tool for studying the niches occupied by species.

We might analogize the total ecosystem of the earth with a great tangled ball of yarn. The tangle results from the reactions, coactions, and interactions of a complex of physical and biotic factors acting upon a complex of living organisms dynamically adjusting in both space and time. In working with this tangle, the major habitat concept helps us to subdivide the ball, and the tag ends of minor habitats which stick out here and there allow us to make some further analysis. Eventually with the extension of these tools and the addition of others we may hope to understand, if never to analyze in detail, the central tangle.

The danger lies, as others have pointed out, in letting our investigatory fire run too lightly over the surface without ever penetrating beneath it. If we content ourselves with superficial listing and description, the preoccupation with habitat can prove completely sterile.

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